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## ON THE FEMALE GENITALIA OF THE MICROLEPIDOPTERA AND THEIR IMPORTANCE IN THE CLASSIFICATION AND DETERMINATION OF THESE MOTHS.

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The female genitalia of the Lepidoptera present, as do those of the males, very complicated structures, which are of great value in the proper classification of this order of insects.

The females of the primitive suborder of the *Lepidoptera*, the *Jugatae*, including the families *Hepialidae*, *Micropterygidae*, *Mnesarchaeidae*,<sup>1</sup> and *Eriocraniidae*, have a single sex opening at the end of the abdomen just below the anal opening, serving both for copulation and for oviposition. This condition obtains also in the order *Trichoptera*, from which the *Jugatae* originated.

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<sup>1</sup> The family *Mnesarchaeidae* consists of a single small New Zealand genus; the female genitalia were described by the late A. Philpott (Trans. N. Zealand Inst., vol. 57, p. 715, figs. 1, 2, and 3, 1926). Because of limited material this conscientious and able worker was unable to satisfy himself about these structures, and his description mistakenly suggests that two genital openings are present. To quote my lamented friend: "The ductus bursa opens in the concavity of this piece" (the sternite of the eighth abdominal segment).

Through the kindness of Dr. G. V. Hudson, of Wellington, New Zealand, the writer has been enabled to study a female of this family (*Mnesarchaea loxoscia* Meyrick) and finds that there is only one genital opening at the end of the abdomen, as in other *Jugatae*. Mr. Philpott's description and figures of these structures are otherwise as accurate as his other work on *Microlepidoptera*.

The other, more specialized suborder of the Lepidoptera, the *Frenatae*, consists of two major groups, according to the type of the female genitalia. The females of one group have, like the *Jugatae*, retained the single sex opening, while the females of the other major group, which comprises by far the greater number of species, have, as is well known, an even more complex genital system with two sex openings, one serving for copulation and one for oviposition.

In the *Jugatae*, two forms of single-opening genitalia are found. In the most primitive families, the last joints of the abdomen are soft and retractible and the genital opening together with the anal opening is surrounded by a more or less bilobed soft ovipositor at the tip of the abdomen. The eggs are laid on the surface of the foodplant or just dropped broadcast near the food, hence there is no need of a piercing ovipositor, and the chitinized rods (the posterior and anterior apophyses) from the last segments forward, which serve for muscle attachment in the higher Lepidoptera, are not developed. Such is the condition found in the *Hepialidae*, *Micropterygidae*, and *Mnesarchaeidae*.

The family *Eriocraniidae*, on the other hand, inserts the eggs into the food plant; the abdomen is strongly chitinized, greatly modified, and terminates in a strong ovipositor, supported by strong apophyses for attachment of muscles.

In the *Frenatae* with single sex opening there are likewise two forms of genitalia, corresponding by and large to the two forms in the *Jugatae*. One group has more or less soft, unspecialized, bilobed and hairy ovipositors, much like those of *Micropteryx*, though the terminal joints have short apophyses and other chitinized modifications of details. The families *Nepticulidae*, *Tischeriidae*, and *Opostegidae* belong to this group and are presumably direct descendants from micropterygid stock.

The other group of *Frenatae* with one sex opening have piercing ovipositors like the *Eriocraniidae*, and are presumably derived from eriocraniid stock. This group consists of the families *Incurvariidae*, *Prodoxidae*, *Adelidae*, *Crinopterygidae*, and *Heliozelidae*.

The insects of both of these groups, the so-called *aculeate Microlepidoptera* (Spüler), possess another archaic character in common with the *Jugatae* in the minute spines (*aculea*) between the scales on the wings, which are actually a part of the wing membrane, not attached in follicles as are the hairs and scales.

This character also is an inheritance from the *Trichoptera*, in which it is prevalent.

It should be realized, however, that of these two fundamental characters the number of sex-openings is absolute and therefore by far the more dependable one. Transition forms must, of course, have existed at some time, but the change is a very ancient one and, as far as we know, no species in the transition stage has survived.

The wing aculeation, on the other hand, is in its nature a character which could be expected to disappear gradually without the necessity of other structural modification, and such is found to be the case. While all the forms with one genital opening possess aculeation, it has become much reduced in area in *Opostega*, and the aculeation has persisted, though much scattered and reduced, in certain forms with two genital openings in the family *Tineidae* and even in some higher families.

The single sex-opening was first pointed out in the genus *Nematois* by N. Cholodkowsky (Über den Geschlechtsapparat *Nematois metallicus* Poda, Zeitschrift für Wissenschaft. Zoologie, vol. 42, 1885) and has been demonstrated since by Willh. Petersen (Mem. de L'Academie Imp. St. Petersburg, series 8, vol. 9, no. 6, 1900) and others in the families *Adelidae*, *Incurvariidae*, and *Nepticulidae*.

A typical American example of the females with single sex opening is found in the Yucca moth, *Tegeticula alba* Zeller (*Pro-nuba yuccasella* Riley), the genitalic complex of which is given schematically in Plate IX, figure 1.

The several oviducts from the large curved ovaries (Ova.) unite into one enlarged oviductus communis (Ovid.), in which the actual fertilization of the eggs presumably takes place. The oviduct narrows into a slender egg-laying tube (Ovid.), which can be extended long beyond the opening of the chitinized, sharp-pointed, and sharp-edged ovipositor (Ovip.) formed by the ninth segment. This segment is prolonged forward into the body in two long, slightly curved, chitinized processes, the so-called posterior apophyses (P. A.), or segmental rods, which serve for the attachment of the muscles which move the ovipositor in and out. The male sperm is introduced through this same egg tube, which at the time of copulation is withdrawn to the end of the ovipositor, and it finds its temporary storing place in the large oval bursa copulatrix (B.), the duct (D.) of which unites with the narrow

tube-like part of the oviduct near the tip of the abdomen in the eighth abdominal segment; this segment is strongly chitinized, and entirely enclosed within the similarly strongly chitinized seventh abdominal segment, from which it can not be protruded; it is prolonged forward into the abdomen in two slender segmental rods, the *anterior apophyses* (A. A.), which serve for muscle attachment. The *ductus bursae* (D.), which thus is also a *ductus seminalis*, has an enlarged part near the middle (E.) with two chitinized rods and covered with strong muscles. This enlarged part may correspond, in function at least, to the *bulla seminalis*, found in some of the groups with two genital openings, or to the *receptaculum seminalis*, and presumably serves the same purpose of temporarily storing and eventually expelling the sperm into the enlarged part of the oviduct. The bursa is large, oval, heavily covered with strong musculature, and contains, in the present species, two opposing, large, striking, star or flower shaped *signa* (Sn.), first described by Hagen (Zool. Anzeiger, 1862). There are a great many variations and modifications of all the characters given; each species has its own peculiar form, but the example given illustrates the common scheme of the genital complex of the group of moths with only one genital opening.

The common European and American Tortricid moth *Cacoecia rosana* L. will serve as an example for the other, numerically much larger group, *with two genital openings*, in the female.

Its abdomen is shown schematically in Plate IX, figure 2. Here we find from the similarly large curved ovaries (Ova.) four oviducts (Ovid.) united into two, and again into one, which leads the eggs into an enlarged *oviductus communis* (O. C.); the oviductus again narrows and terminates at the tip of the abdomen just below or uniting with the anal opening of the digestive system (A.); both are surrounded at their terminus by two soft, flattened, hairy ovipositors (Ovip.), varying in form in different species.

The entrance, the *ostium* (Ost.) to the *bursa* (B.), is widely separated from the egg-laying opening and is found on the ventral side in the intersegmental skin between the seventh and eighth segments, normally surrounded by a chitinized area (the genital plate). Through this opening copulation takes place, the long tube-like male penis penetrating through it, and all the way through the sometimes very long *ductus bursae* (D.) into the

capacious bladder-like *bursa copulatrix* (B.), where the sperm is temporarily desposited. The bursa, in the species pictured (and in the entire *Cacoecia* group), is armed on the inside of the wall with a strong, curved, chitinous spine, the *signum* (Sn.); in other genera the signum has a different, sometimes a very different, form.

The *ductus bursae* (D.) is connected with the *oviductus communis* (O. C.) by a narrow tube, the *ductus seminalis* (D. S.), which in the species under consideration (and in all *Tortricidae*) has near its middle a large, blind, bladder-like enlargement, the so-called *bulla seminalis* (B. S.), connected by a short narrow tube, *ductus bullae* (D. B.).

Opening into the oviductus communis is the *receptaculum seminalis* (R. S.), a highly specialized, spiraled, last storing place for the male sperm, before it fecundates the eggs as they pass out into the *oviductus communis* (O. C.). Near the end of the oviduct the eggs are given an adhesive coating secreted from two large glands, *glandulae sebaceae* (Gl.), with a common outlet.

The example given shows the general scheme of the female sexual organs in the Lepidoptera with two sex openings, but the details vary greatly in the different families and offer excellent characters for the differentiation of families and genera, as well as for the species.

It is obvious, without discussion, that such fundamental anatomical differences as presented in the two main groups with one and with two sex openings and the consequent internal differences in structure must be expressed in a natural classification.<sup>2</sup>

This has already been effected by Spüler, by his superfamily "*Tineides aculeatae*,"<sup>3</sup> erected on the other archaic character, the

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<sup>2</sup> Chapman, who believed the single genital opening was confined to the genus *Micropteryx*, even proposed a new order for it—*Zeugloptera*—on this character alone.

<sup>3</sup> *Tineides aculeatae* is an unfortunate term, first, because it does not conform to superfamily terms in general use, and secondly, because the species comprising the group are not "*Tineides*." I propose to substitute the two superfamily names already in use, *Nepticuloidea* for the families with more or less soft ovipositor in the female, and *Incurvarioidea* for the families with highly specialized piercing ovipositor.



aculeate wings,<sup>4</sup> but it is very inadequately expressed in our English literature, as represented by Meyrick's Handbook and our American checklists. W. T. M. Forbes, however, has utilized these fundamental characters, in part, in his Lepidoptera of New York, 1923.

Any grouping of the Microlepidoptera which does not sharply separate the one-genital-opening forms from the two-genital-opening forms, but which unites some members of each main division within the same family, is clearly unnatural.

The study of the female genitalia, therefore, proves that Meyrick's twelve "phyla" do not express equivalent systematic concepts and that his "tribe" *Tineoidea* is unnatural, because it includes families of both main groups (with single, and with double genital opening), while one family with single genital opening, the *Nepticulidae*, has been singled out, inconsistently, as a separate "phylum."

The application of these studies then give us the more natural arrangement, as shown on Plate XIII, which, with slight modifications, much resembles the phylogenetic table based on wing characters (Busck, Proc. Ent. Soc. Washington, vol. 16, pl. 2, 1914).

As indicated, it is not only the major difference of the one or two genital openings which makes the female genitalia a valuable aid in the classification of Lepidoptera. The modifications of the minor details of the genitalia, such as the form of the *ostium*, the length of the *ductus bursae*, the type of the *signum*, the position of the *ductus seminalis*, the presence or absence of a *bullula seminalis*, and the form of the *ovipositor*, are all useful in the classification, and taken together commonly at once indicate the systematic position of the species.

The *ostium* is usually cup-shaped, margined by a genital plate of various form, more or less flush with the abdominal wall (*Tortricidae*, *Phalonidae*, *Stenomidae*, *Oecophoridae*, and others), but in some groups (*Cosmopterygidae*, *Scythridae*, *Amydria*, and

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<sup>4</sup> One of the genera included by Spüler under the *Tineides aculeatae*, *Meessia* Hoffman (type *vinculella* Herrick-Schaeffer) is misplaced. It has two genital openings and has just a trace of wing aculeation, such as commonly persists in some Tineid genera and even in higher groups. Spüler correctly divided the genus and placed *argentibaculella* as the type of his new genus *Infurcilinea* in the nonaculeates next to *Tinea*. *Meessia* likewise belongs in the *Tineidae* very close to the American genus *Eudarcia* Clemens.

*Meessia*), the *ductus bursa* is protruded outside of the body wall as a chitinized tube (usually asymmetrically placed so as to permit copulation from only one side) with the *ostium* at its tip (Plate XII, fig. 16).

The *genital plate* varies in outline in different species; it may be circular, oval, square, or triangular or otherwise; its surface may be smooth, or wrinkled, or pitted, but it is constant within the species.

The *ductus bursae* may be very short, bringing the bursa close up to the *ostium* (*Phaloniidae* and others, Plate 2, fig. 2), or it may be longer, sometimes very long, nearly twice the length of the abdomen, which necessitates a curling or looping of the ductus. In such case, the ductus is commonly chitinized on one side as a guide to the penis (plate XI, fig. 11); in other forms, the ductus is looped once or twice upon itself (*Sparganothidae*, Plate XI, fig. 8) or tightly spiraled (*Smicrotes*, Plate X, fig. 1).

The *ductus seminalis* more commonly arises from the ductus bursae and in such case the point of junction, close to the ostium, or close to the bursa, is significant. In some families (*Gelechiidea*), the *ductus seminalis* is emitted from the bursa.

The *bursa* may be single or double, large or small, round or elongate or irregularly pouched according to the family.

The *signum* may be single or double or absent. These characters are normally of generic significance, sometimes of family value. The signum may be a single sharp thorn with bulbed base (*Cacoecia*, Plate IX, fig. 2), or two small spines (*Laspeyresia*); or it may be a stellate plate (*Peronea*, Plate XII, fig. 17); a flat band (*Amorbia* and *Coelosthathma*, Plate X, fig. 6); an elongate, dentate band or rope (*Sparganothis* and *Cnephasia*, Plate XI, figs. 7, 8, and 9); or a more elaborate structure like those in *Gelechiidae*, *Stenomidae*, and other families (Plate XII, figs. 13, 14, and 18).

The bursa wall itself may be evenly thick-skinned or may be in whole or part thickened or covered on the inside with short spines, granules, or chitinized plates (*Eulia*, *Amorbia* and *Sparganothis*, Plate X, fig. 6; Plate XI, fig. 8), or heavily armored with strong spines (*Phalonia*, Plate X, fig. 2).

In many species, the exceedingly extensible penis of the male reaches, during copulation, all the way through the ductus bursae into the bursa, where the spermatozoa are deposited and commonly completely fill it. The extension of the penis is similar in

action to the blowing out on an inverted finger in a glove, unrolled from within by blood-pressure, but the penetration of this soft organ through the sometimes very long and looped female ductus can hardly be effected by blood and air pressure of the male alone; it is probably aided by peristaltic motion and suction in the female organ, the bursa being deflated by muscle pressure before copulation and a semivacuum thus created, when the muscles relax.

In many (most) groups of Microlepidoptera, the penis bristles with a formidable armature of sharp spines, the *cornuti*, sometimes fixed and withdrawn again with the penis after copulation, but commonly loosely attached and left in the female bursa (*deciduous cornuti*). These deciduous spines are normally flattened, very sharply pointed, and often nearly as long as the diameter of the female bursa, in which they remain with the spermatozoa after the penis is withdrawn. The purpose of these "lovethorns" is not definitely known. Stitz believes they serve to pierce and break up the congealed surfaces (spermatophores) around the spermatozoa and thus liberate these for their further progress into the ductus communis. The writer is inclined to this view, which, however, is strongly contested by Petersen, who insists that the spermatophores must remain unbroken to fulfill their purpose, as he sees it. He believes that the signum helps to hold in place the smooth-surfaced spermatophores, but this would not explain the deciduous cornuti. Dampf suggests that the cornuti, as well as the signum in the female bursa, serves to excite and stimulate sexual action. Whatever their function, it is indeed remarkable that these exceedingly sharp and stiff spines (which in different species number from one to more than a dozen) are capable of serving their purpose without piercing the comparatively soft and thin skin of the bursa.

In certain Macrolepidoptera (butterflies and Noctuids) Petersen and others have convincingly demonstrated actual containers or capsules for the spermatozoa, the *spermatophores*, which Petersen contends are formed in their final and definite shape in the male penis. According to Petersen these spermatophores are chitinized and remain intact in the female bursa. They are more or less bottle-shaped and the open neck is, in certain forms, exactly the length of the distance from the bursa to the ductus seminalis, into which their contents are squeezed by muscle pressure on the bursa, leaving the empty shell of the spermatophores in the bursa.



In the Microlepidoptera I have not been able to find any such specialized structures, and there at least I believe that the so-called spermatophores are not separate, chitinized structures, but merely the coagulated surface of the mucous or gelatinous fluid surrounding the spermatozoa. That these congealed surfaces, however, in some species, attain a certain toughness and may require the sharp spines of the penis and bursa to tear them open is commonly demonstrated by their persistence through the preparation for the slide-mount, after which they may at times be found intact, either yet filled with spermatozoa or as empty bags within the bursa. This persistence through the boiling in caustic potash certainly suggests the presence of chitin, but the spermatozoa themselves, in preparations of both male and female genitalia, likewise resist to a certain extent the action of potash, and both spermatozoa and spermatophores react alike to color dyes.

The *ovipositor*, in the forms with two genital openings, normally consists of two soft, flattened, hairy lobes, surrounding the anal opening and the outlet for the oviduct. The form of these lobes is constant within the species. In some genera, these lobes are highly specialized, curved, with strongly spined folds (*floricomous ovipositors* Pierce), possibly useful in covering the egg with scales from the abdomen (*Cnephasia* and *Argyrotoxa*, Plate XI, figs. 7 and 9). In other genera, the two lobes are facing each other and partly united into a tube, which, with the long, soft, telescopic last segments of the abdomen, enables the insertion of the eggs into crevices of bark or fruits or into soft and loose material, as cloth, birdnests, and the like (*Tinea* and others). In still other groups, the two lobes of the ovipositor are strongly chitinized and more or less united into a sharp cutting or piercing blade-like organ, which, backed by the chitinized posterior abdominal segments, enables the insertion of the eggs into the food-plants by cutting or piercing the surface (certain *Gelechiidae* and others). This form of ovipositor, however, retains the hairs of the lobes and is merely a chitinized modification of the soft telescopic form just described; it is constructed very differently from the piercing ovipositor found in the aculeate, one-genital-opening forms, as described previously (*Tegeticula*), in which the strongly chitinized eighth segment can not protrude from the seventh and in which the ovipositor (ninth segment) is a completely chitinized, sharply pointed tube, devoid of hairs.

The form of the *ovaries*, of the *oviducts*, and especially of the *receptaculum seminalis*, also yields important characters; the

number and relative distance of the spiralled windings of the latter, for example, are constant for the species; but these soft structures are easily lost in the potash treatment and for practical purposes we rely on the other more readily preserved structures of the internal anatomy, the bursa and its accessories.

Finally, the more secondary sexual characters, like cushions of peculiar scaling (Plate X, fig. 4), hairtufts concealed at rest in deep pouches and expansible during sexual incitation, afford some aid in the grouping of Microlepidoptera, but are, of course, of no such taxonomic significance as the structure of the genitalia themselves.

Aside from their great value in the technical taxonomic work of classifying the Microlepidoptera, the female genitalia, as well as those of the males, have a very important practical application, constantly utilized in the determination of material sent in by the field agents of the U. S. Bureau of Entomology, who are studying the economic aspects of insects injurious to crops, like the pink bollworm, the codling moth, and the oriental fruit moth, to give well-known examples.

Such specimens are more often than not in exceedingly poor condition for determination, commonly necessarily so, because of the difficulty of catching and preserving these delicate moths under adverse field conditions, where the study of their biology or of the best methods for destroying them are the prime objects. This holds particularly in cases where light or bait attraction is tested against injurious species and the moths are caught in various traps, normally waterpans with a surface film of oil or baited with molasses and even more so in the investigations of the spread of injurious insects, by flight or air-currents, where the moths are caught on flypaper attached to rapidly moving airplanes.

The moths secured by such methods are necessarily in poor condition, normally devoid of scales, and often with legs, palpi, and wings broken or lost—sometimes mere fragments, apparently unrecognizable. The definite determination of those catches, however, is of course essential in order to decide whether the insects caught are the injurious species intended for investigation and combat, or merely some stray species of no economic value.

While all the appendages and the color of such specimens commonly are lost, and with them the characters on which we formerly relied for their determination, the body is normally intact and the genitalia may be extracted and mounted on a slide in perfect condition for examination under the microscope.

With the gradual and constantly increasing accumulation of more than 10,000 carefully made, definitely determined and classified slides of the genitalia of injurious species, as well as of their innocuous relatives and associates, it is now, in most cases, a comparatively simple task to identify with certainty the insect "criminals," national and international, females as well as males, by their "fingerprints."

EXPLANATION OF PLATES.

PLATE IX.

Fig. 1. *Tegeticular alba* Zeller.

Schematic outline of female abdomen and genital structures in moths with *one* sex opening.

Fig. 2. *Cacoecia rosana* Linnaeus.

Schematic outline of female abdomen and genital structures in moths with *two* sex openings.

ABBREVIATIONS USED IN FIGURES.

Nos. 1-9	Abdominal segments.
Ova.	Ovaries.
B.	Bursa copulatrix.
Sn.	Signum.
D.	Ductus bursae.
Ovid.	Oviducts.
A. A.	Anterior apophyses.
P. A.	Posterior apophyses.
E.	Enlarged part of ductus bursae.
B. S.	Bulla seminalis.
D. B.	Ductus bullae.
D. S.	Ductus seminalis.
R. S.	Receptaculum seminalis.
Ost.	Ostium.
Ovip.	Ovipositor.

PLATE X.

FEMALE GENITALIA.

Fig. 1. *Smicrotes peritana* Clemens.

Genotype.

Fig. 2. *Clysia ambiguella* Hübner.

Genotype.

- Fig. 3. *Carposina berberidella* Herr.-Schaeff.  
Genotype.
- Fig. 4. *Templemania animosana* Busck.  
Genotype.
- Fig. 5. Undenuded tip of abdomen, with specialized sex scaling.  
*Templemania animosana* Busck.  
Denuded tip of abdomen.
- Fig. 6. *Amorbia humerosana* Clemens.  
Genotype.

PLATE XI.

FEMALE GENITALIA.

- Fig. 7. *Ablabia osseana* Scopoli.  
Genotype.
- Fig. 8. *Sparganothis pettitana* Robinson.
- Fig. 9. *Ablabia argentana* Clerck.
- Fig. 10. *Rhacodia emargana* Fabricius.  
Genotype.
- Fig. 11. *Choristineura parallela* Robinson.

PLATE XII.

FEMALE GENITALIA.

- Fig. 12. *Mompha conturbatella* Hübner.  
Genotype.
- Fig. 13. *Isotrias rectifasciana* Hübner.  
Genotype.
- Fig. 14. *Polylopha epidesma* Lower.  
Genotype.
- Fig. 15. *Pseudatteria rivularis* Butler.
- Fig. 16. *Cosmoptyx eximia* Haworth.  
Genotype.
- Fig. 17. *Peronea nigrolinea* Robinson
- Fig. 18. *Caenognosis incisa* Walsingham.  
Genotype.

(The drawings were made by Mrs. Eleanor A. Carlin under the author's supervision from slides prepared by him.)

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